The associations of Algae with arthropods

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> « The number of living creatures of all orders, whose existence intimately depends on the kelp [*Macrocystis pyrifera*]... is wonderful... innumerable crustacea frequent every part of the plant ».
>
> Charles Darwin
> *The Voyage of the Beagle*

1. INTRODUCTION

This is the second in a series of review papers intended to discuss the various interactions between arthropods and lower green plants. The first part of this series (Gerson, 1969) dealt with the associations between arthropods and mosses, and other instalments, discussing the relationships of these animals with lichens and ferns, respectively, are in preparation.

It is not the intention of these reviews to be comprehensive. Rather they are meant to draw attention to some areas of ecological research which appear to be little appreciated, lying, as they do, between the various academic disciplines. The relationships between arthropods (and especially insects) and the higher plants have been extensively investigated, mostly because of the economic aspects involved. Feeding of crustaceans on algae in the seas and freshwater bodies has also been relatively well studied, for similar reasons. Other interrelationships between the arthropods and the algae (and the mosses, lichens and ferns), on the other hand, do not appear to have been summarized before. It is the purpose of these reviews to present an extensive, as wide as possible, panorama of these associations.

Some qualifications should be stated at the onset. Wherever recent pertinent reviews are available, pertaining to marine plankton (Raymont, 1966; Wimpenny, 1966), phytoplankton production (Strickland, 1965), zooplankton production (Conover, 1968; Mullin, 1969) or feeding mechanisms (Jörgensen, 1966), reference

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will be made to them, and mention of these subjects will be as brief as possible. Many authors do not specifically refer to algae or to crustaceans in their papers, but rather to phytoplankton and zooplankton, respectively. Some use of the latter nouns will also be made here, but in every case they refer to algae and crustaceans as meant in the quoted papers. Finally, some repetition of material is unavoidable, as certain relationships involve more than one type of interaction.

Another problem arises in dealing with some of the achloric algae, which are also categorized among the Protozoa (see KUDO, 1954). It was finally decided to note all species which FRITSCH (1956, 1959) included in his monograph.

2. ARTHROPOD FEEDING ON ALGAE IN AQUATIC HABITATS

Diverse arthropods feed on algae in the sea, the littoral and in freshwater habitats. In the sea copepods, cladocerans and (in colder waters) euphausiids predominate (JÖRGENSEN, 1966; WIMPENNY, 1966; MAUCHLINE and FISHER, 1969). Representatives of many groups feed on intertidal algae (HAGERMAN, 1966; JANSSON, 1967), and cyclopoid copepods as well as numerous insects graze on these plants in rivers and lakes (CHAPMAN and DEMORY, 1963; FRYER, 1957; NEEL, 1968 and many others).

2. 1 Modes of feeding

Feeding mechanisms employed by aquatic arthropods were reviewed by JÖRGENSEN (1966). Two main groups of mechanisms are involved, namely suspension feeding and direct grazing. Some crustaceans utilize both, the same animal being capable of suspension-feeding on small unicellular algae and grazing on large ones, although not simultaneously (CONOVER, 1968). Other, less common modes of feeding are by mining galleries in algae or by sucking their juices. The former is employed by some copepods (GREEN, 1963) and midges (BROCK, 1960; SOURIE, 1962), whereas ostracods of the subfamily Paradoxostominae and several haliplid beetles feed by sucking algal juices (HAGERMAN, 1966; SEEGER, 1971).

The feeding apparatus evolved by copepods, cladocerans and other arthropods which subsist on algae in suspension was described in detail by JÖRGENSEN (1966), and the mouthparts of algae-feeding insects (like mayflies and caddis flies) are elaborated in standard entomological textbooks (i. e., IMMS, 1957). Modifications for different modes of feeding on algae are found even within a single genus, as **Seeger** (1971) demonstrated for species of the beetle *Haliplus*. Some of these have sharp, pointed mandibular teeth, adapted for puncturing cell walls and subsequently sucking their contents, whereas others have robust, rounded teeth, suitable for biting and chewing.

Some arthropods feed exclusively on algae, but many others, to be discussed in the next section, also utilize additional diets.

2. 2 *Seasonal, diurnal and stage-dependent feeding*

The food preferences of many aquatic arthropods appear to depend more on availability than on any other single factor. **Paine** and **Vadas** (1969) postulated that such availability may have been more important in the evolution of food preferences of benthic invertebrates than food value per se. **Mauchline** and **Fisher** (1969) concluded that the food of euphausiids consists mainly in whatever is available, and **Fryer** (1957) noted the same in regard to freshwater cyclopoid copepods.

Some arthropods therefore feed on algae only during spring and summer, when these plants are more abundant, being predaceous of detritus-feeders during periods of relative algal scarcity. Such feeding behavior has been reported for marine euphausiids (**Mauchline** and **Fisher**, 1969) and crabs (**Longhurst**, **Lorenzen** and **Thomas**, 1967) and for the freshwater-inhabiting larvae of various insects, including caddis flies, mayflies and stoneflies (**Chapman** and **Demory**, 1963; **Jones**, 1950). **Zahar** (1951) found that diatoms were predominant in the guts of stream-dwelling black fly (simuliid) larvae during spring, larger algae during summer and plant debris were the main food in winter.

Neel (1968) noted that various stream invertebrates (among them numerous arthropods) favored growths of *Lemanea* during spring and early summer and those of *Phormidium* in summer and early autumn. He did not however know whether the algae were actually preferred, or favored only because their growths were present during the appropriate seasons.

Diurnal feeding on algae has been reported in regard to some Black-Sea inhabiting amphipods (**Greze**, 1968); *Dexamine spinosa*, *Amphithoe vaillanti* and *Gammarellus carinatus* feeding mainly during the dark period, *Gammarus locusta* in the morning. Vertically migrating crustaceans feed in the upper water layers only at night, inhabiting deeper layers and not feeding at all during the day (**Petipa** and **Makarova**, 1969). Such feeding behavior was postulated by CONOVER (1968) to actually help in conserving algal populations. Another type of diel feeding behavior was noted in regard to the mayfly nymph *Paraleptophlebia* (CHAPMAN and DEMORY, 1963), which feeds on stream-bottom detritus by day, and on upper-layer algae by night.

Many insects which have aquatic juvenile stages (e. g. Ephemeroptera, Plecoptera, Trichoptera, some Diptera) consume algae only during these stages (CHAPMAN and DEMORY, 1963; IMMS, 1957). Some crustaceans, like the isopod *Dynamene bidentata* and the wheel shrimp *Penaeus japonicus*, feed on algae only during their nauplius stages (HOLDICH, 1968; IDYLL, 1965).

2. 3 Alga-arthropod food chains

Ecologists have long acknowledged the role of the crustaceans in feeding on the phytoplankton (a major part of which consists of algae) in oceanic food chains which lead to the production of commercial fish (CLARKE, 1954; ODUM, 1953; MAUCHLINE and FISHER, 1969 and many others). Commercial fish, often unable to utilize algae directly as food, must depend on animals of intermediate size, like the copepods and euphausiids (CLARKE, 1954). This author visualized such aquatic arthropods as « miniature harvesting machines » which pack microscopic plant (algal) cells by feeding, until they represent parcels of food of sufficient size for the larger animals. Many additional aquatic grazers — sea urchins, molluscs and others — also feed on algae, but only in coastal waters. The crustaceans — mainly the copepods — remain the chief link in the food web between the plants and the fishes in the oceans.

In temperate and tropical waters food chains are long and complicated, with a great resultant dissipation in energy between the various levels (BERRILL, 1966). Acting upon such considerations, PEQUEGNAT (1958) advocated utilization of the diatom-krill (the euphausiid *Euphausia superba*) — whale food chain which occurs in Antarctic waters. MURPHY (1962) described the krill as the key organism in the shortest (and thus the most economic) food web in the Antarctic. It is economical because the krill feeds directly on the diatoms, and in turn is large enough to be directly fed upon by seals and whales.

The commercial manipulation and utilization of short food chains in fish ponds was described by ODUM (1953). The number of « side food chains » is reduced as much as possible. The producers are restricted to one group, the floating algae, growth of other aquatic algae being discouraged. The encouraged plants are grazed by arthropods (and various worms), which then serve as food for fish. SASA, KUNIEDA and TAMIYA (1960) concluded from their experiments and calculations that culturing the water flea *Daphnia* on *Chlorella* may well be a most efficient system of converting plant protein into animal protein. The utilization ot insect larvae (instead of crustaceans) as algal grazers for the intermediate stage in fish production was advocated by ZARNECKI (1968), who believed that in this way great quantities of valuable fish protein may be quickly produced in relatively small surface areas.

In some cases epiphytic diatoms, growing on larger algae such as *Fucus* and *Cladophora*, serve as the base of food chains. The primary consumers in such food chains include many arthropods (HAGERMAN, 1966; JANSSON, 1967). « The importance of these epiphytes as a food source for the fauna associated with *Cladophora* is outstanding » stated JANSSON (*l. c.*), who presented evidence that epiphytic diatoms were essential for isopod juveniles.

Laboratory workers have often used the relatively-simple and measurable alga-crustacean food chain association in studies on ecological energetics, the most complete data of this kind being available for *Daphnia* feeding on various algae (SLOBODKIN, 1962).

2. 4 *The passage of various compounds through the alga-arthropod food chain*

The primary consumers not only concentrate and metabolize algal food to a form suitable for the secondary consumers, but may also transfer other compounds. Pristane (2, 6, 10, 14, tetramethylpentadecane) is an isoprenoid hydrocarbon which occurs in abnormally high concentrations in some crude oils (BENDORAITIS, BROWN and HEPNER, 1962). Its presence there is considered evidence for a biological contribution of hydrocarbons in nature (AVIGAN and BLUMER, 1968). The substance was recovered from some animals, including copepods. Studying the origin of pristane in *Calanus*, AVIGAN and BLUMER (1968) showed that this hydrocarbon was synthesized in the bodies of the copepods from labelled phytol-U-^{14} C present in the ingested algae (*Thalassiosira*). The inference is that algal chlorophyll probably breaks down is the copepods'bodies to the porphyrin and phytol parts. It is the latter, a diterpenic alcohol, which has been shown to serve as the pristane precursor. In this case the food relationship between algae and copepods forms the source for a prominent petroleum constituent, bearing also on theories regarding the origin of petroleum (Bendoraitis *et al.*, 1962).

Other materials moved up through these food chains may be inhibitory or toxic. A substance was discovered which inhibits the anterior gastrointestinal microflora of penguins (Sieburth, 1961, 1968). This substance, subsequently identified as acrylic acid, was traced to the phytoplankton-laden stomach contents of the krill, which constituted the only diet of the penguins. Acrylic acid, a « broad spectrum » antibiotic, was later discovered in blooms of the chrysophycean alga *Phaeocystis pouchetii,* as well as in some other algae. This compound was not toxic to the grazing euphausiids.

King (1964) has shown how cesium-137, a potentially dangerous fission fall-out product from nuclear tests, is taken up by *Chlamydomonas. Daphnia* then feeds on the radioactive algae, and is later eaten by bluegill fingerlings (*Lepomis macrochirus*), the cesium thus moving up the food chain from algae *via Daphnia* to the fish. Radioactive carbon was utilized in many experiments meant to estimate arthropod feeding on algae (Slobodkin, 1962; Lasker, 1960). Brock, Wiegert and Brock (1969) incorporated labelled sodium carbonate into algae on which two ephydrid flies (*Paracoenia* and *Ephydra*) fed, and demonstrated that the algal radioactivity was converted to a biochemically different form in the insects' bodies. The differential susceptibility of algae to insecticides has been studied (Menzel *et al.*, 1970), and some of the resistant plants are also capable of considerable biological concentration of these compounds (Vance and Edwards, 1969). The contaminated algae thus form a danger to the much less resistant arthropod grazers (Vance and Edwards, 1969). This subject will be further discussed in section 8. 2.

2. 5 *Phytoplankton-zooplankton interactions and « superfluous feeding »*

The interactions between the phytoplankton and the grazing zooplankton, such as copepods and cladocerans, have several times been reviewed (Mullin, 1969; Raymont, 1966; Wimpenny, 1966 and others). Many cases are known where arthropods had profound effects on algal populations, causing their virtual depletion or disappearance (Cushing, 1964; Van Landingham, 1964; Zarnecki, 1968). Martin (1965) has described a direct, regulating relationship between copepod grazers and the peaking (« blooming ») of algal populations. This author showed that in Narragansett Bay (in the northeastern United States) algae (mostly the diatom *Skeletonema*) bloomed in winter and spring. During the latter season populations of copepods (*Acartia*) rapidly grow and begin to graze down the diatom bloom. This situation prevails till winter when grazing pressure is relieved; and it is then that blooms begin again.

The great fluctuations in crustacean populations grazing on algae, referred to above, appear to occur more in temperate climates and at high altitudes than in the tropics. In tropical regions phytoplankton productivity varies little throughout the year, the steady state of this production being assumed to be maintained mostly by the grazing activity of the zooplankton (JÖRGENSEN, 1966; RAYMONT, 1966). The regular succession changes occurring in pelagic phytoplankton populations and their associated feeders (mostly copepods) were discussed by MARGALEF (1967), who stated that animals are an important factor in controlling the speed and direction of these successions (see also MULLIN, 1967).

The occurrence of such large-scale grazing by the zooplankton implies that the populations of the animals would peak concomitantly with those of the phytoplankton. Though this does occur sometimes, many observations have indicated that phytoplankton and zooplankton « pulses » are often well separated (RAYMONT, 1966; Van LANDINGHAM, 1964). Two sets of theories have been presented to account for these phenomena. HARVEY (1934) attributed them to accelerated zooplankton grazing, whereas HARDY (1936) argues that the phytoplankton release inhibiting substances into the surrounding aquatic medium. Much information has accumulated in support of both theories (see references in previous paragraph, and also BAINBRIDGE, 1953; LUCAS, 1961; RYTHER, 1954; SIEBURTH, 1968), and they will not be further discussed.

Arthropods have been reported to be involved in some other mechanisms which may result in great changes of algal abundance-although BROOK (1955) complained that the aquatic fauna (especially insects) is often overlooked in ecological studies of fresh water algae. GIBOR (1956) observed heavy *Stichococcus* blooms in evaporation ponds. On feeding that alga, together with another, *Dunaliella*, to the brine shrimp *Artemia* and to the copepod *Tigriopus* he observed that only the latter alga was grazed. As a result *Stichococcus* became dominant when the two algae were cultured and offered together to the animals. GIBOR (*l. c.*) suggests that the scarcity of some species of zooplankton in phytoplankton-rich waters may therefore be explained by the nutritional unsuitability of some algae to the grazers. FRYER (1957) reported that while diatoms are invariably digested by copepods, small algae like *Scenedesmus* and *Cosmarium* emerge undamaged from the animals' anus. Consequently the returned, undigested algae may replace the more nutritionally-valuable ones. Similar observations were noted by BROOKS (1969).

BROOKS and DODSON (1965) described the effect that predation on zooplankton by fishes exerts on these plants. When such predation occurs at low intensity, the small phytophagous organisms (rotifers and small cladocera) tend to be competitively eliminated by larger grazers, such as calanoid copepods and large Cladocera. At such periods efficient grazing results in relatively small algal populations. However, when fish predation becomes intense, more of the larger crustaceans are eaten and thus become scarce. Consequently the small, less efficient grazers become dominant. At these times the numbers of both small and large algae will greatly increase, as the remaining grazers cannot utilize the plants as fully as can the larger crustaceans.

The term « superfluous feeding » (BEKLEMISHEV, 1962) has been introduced to describe feeding behavior in zooplankton feeding on rich phytoplankton populations. In these instances the animals ingest voraciously, more than they can digest and assimilate, and void many undigested algal cells. The problem was reviewed by CONOVER (1966) who found that the proportion of assimilated food was related neither to the amount of food (algae) offered (to *Calanus*) nor to the amount ingested by the copepods. However, algae with a low ash content seemed to be more completely assimilated than those with a large amount of ash. From these and other results CONOVER (*l. c.*) concluded that « superfluous feeding » does not normally occur under natural conditions.

Whatever the meaning of « superfluous feeding », crustaceans grazing in rich phytoplankton beds do void many undigested algal cells (CUSHING, 1964; HARVEY, 1963). It is tempting to postulate on some ecological benefit accruing to the feeders from this type of feeding. Its significance for the regeneration of organic nutrients in the sea was discussed by CUSHING and VUCETIC (1963). Also, as some « water blooms » are lethal for the zooplankton (see below), the animals may be ingesting more than their needs so as to reduce algal populations. The data presented by ENRIGHT (1969) concerning zooplankton grazing rates in the sea off California lends support to this hypothesis. The average grazing rate represented as much as 40-50 percent of the standing crop, implying very rapid phytoplankton turnover. This situation was believed to be quite unstable, as even relatively small imbalances between grazing and algal division, if persisting for several days, could lead to many-fold increases in algal abundance. As such changes could well lead, in regard to certain algae, to « water blooms », the intensive feeding recorded may have direct survival value for the grazers themselves.

2. 6 *Various effects of algal diets on arthropods*

As noted above, the availability of algae may determine whether or not they be utilized as food by various arthropods. The abundance of these plants may also affect the distribution of the feeders. Thus SCOTT (1958) noted that two trichopterans (caddis flies) occurred in a river mainly on the upper face of stones rather than on their underside, because the illuminated upper face supports the most abundant algal growth, on which they feed. ULFSTRAND (1967) made similar observations in regard to some Lapland freshwater insects (among them also several predators), concluding that the microdistribution of these animals appears to be more closely related to food than to any other factor.

The amount of algae eaten may affect the body size of the arthropod grazer, its chemical composition and even its behavior. The copepod *Diaptomus gracilis* was believed by SMYLY (1968) to be larger in shallow water because of the greater accessibility of benthic and littoral algae there. Conversely, when some algae become scarce, as occurs in certain polluted waters, the dependent arthropods may starve and their populations may diminish (HYNES, 1960). The effect of the algal amount eaten on the C/N ratio in *Calanus* was studied by OMORI (1969). In subtropical and tropical waters, where, as noted above, grazing occurs at a fairly uniform rate throughout the year, the C/N ratio is also rather even. But in subarctic waters, following phytoplankton blooms, the C/N ratio increases as the feeding copepods store fat in their bodies. The osmoregulation of the shore-inhabiting isopod *Ligia oceanica* is maintained by feeding on *Fucus*, as the salt content of this brown alga compensates for the insufficient salinity of the substrate (JÖNS, 1964).

Feeding on algae by barnacle (*Balanus* and *Elminius*) nauplii had a pronounced negative effect on the latters' phototactic behavior (SINGARAJAH, MOYSE and KNIGHT-JONES, 1968). This was observed whether or not the surrounding water contained algal metabolites. The change in behavior was believed to be of selective advantage, as such would result in well-fed individuals leaving the phytoplankton-rich waters for darker conditions, where the animals would be less exposed to visually-directed predation (SINGARAJAH *et al.*, 1968).

2. 7 *The nutritional value of algae for arthropods*

Vegetable matter — mostly algae — is believed to be the most important food source for the majority of crustaceans in the seas (MARSHALL and ORR, 1960). The algae obviously supply the feeding arthropods with most of their required nutrients though some growth factors may be at suboptimal levels (CORNER and COWEY, 1968). Phytoplankton is regarded as the main source of lipid-soluble vitamins for the Crustaceae (FISHER, 1960). Evidence is accumulating that arthropods are incapable of cholesterol synthesis (WHITNEY, 1970; ZANDEE, 1967). The algae, which have an abundance of diverse sterols (GOAD, 1970; PATTERSON, 1969 and others), may thus supply this necessary nutrient. The metabolic pathways in the transition of algal lutein and ß-carotene through the intermediate canthaxanthin to the crustacean astaxanthin have been followed in several recent studies (CAMPBELL, 1969; HATA and HATA, 1969). The pebble crab, *Cycloxanthus novemdentatus*, feeds on coralline algae which contain lime, which is then utilized for shell formation (KNUDSON, 1959).

2. 8 *Rearing arthropods on algae under controlled conditions*

Although many arthropods feed on algae, very few have actually been reared in the laboratory for extended periods on bacteria-free unialgal cultures. PROVASOLI, SHIRAISHI and LANCE (1959) and SHIRAISHI and PROVASOLI (1959) reported on the culturing of the copepod *Tigriopus* and the shrimp *Artemia* in axenic algal cultures. Only *Monochrysis lutheri* could sustain the copepods for as long as 18 generations. Monocultures of other algae, such as *Platymonas, Isochrysis, Chroomonas* and *Rhodomonas,* carried the animals through only a few generations and then ceased to support their growth. However, copepods kept on mixed algal cultures, such as *Rhodomonas* and *Isochrysis* together, appeared to be sustained indefinitely. Similar results were obtained with *Artemia* by PROVASOLI *et al.* (1959). These authors concluded that certain algal monocultures can supply nearly all the necessary nutrients to the animals, but some micronutrient or growth factor occurs at only suboptimal levels, causing the populations to decline. Another possibility discussed (SHIRAISHI and PROVASOLI, 1959) was the overproduction of some metabolites, e. g. toxins. However, these authors showed that the addition of vitamin B factors (and/or glutathione) compensates for the observed deficiencies, as does a mixed-algae food, or an algae-and-bacteria food. Prolonged rearing of copepods on mixed-algae diets was also reported by GILAT (1967), NEUNES and PONGOLINI (1965), ZILLIOUX and WILSON (1966) and others, whereas the insufficiency of some algae for the laboratory rearing of *Daphnia* was discussed by TAUB and DOLLAR (1968). The conclusion of most of these authors is that no single alga meets all requirements, as optimal amounts of essential micronutrients are not all present in any one alga (CORNER and COWEY, 1968). Therefore single algal diets have to be supplemented by other algae, bacteria or animal food. Their results obtained by LAKE (1969), while working with the anostracan *Chirocephalus*, and by BOOKHOUT and COSTLOW (1959), when studying barnacles, fall within the same pattern.

As many crustaceans are known to feed on algae, the commercial rearing of the former often involves culturing the latter. *Daphnia* has frequently been utilized for insecticide bioessay. Appropriate methods for its mass-rearing were described by DEWEY and PARKER (1964), who found that *Scenedsmus obliquus* was a slightly better diet than yeasts, but that best results were obtained when both foods were offered together. IDYLL (1965), writing about commercial shrimp (*Penaeus japonicus*) farming in Japan, noted that the protozoeal stages of the shrimp are supplied with the diatom *Skeletonema costatum*, which is separately monocultured in special tanks. The mysis stages of *Penaeus* feed on animal food (see also WEBBER, 1968).

2. 9 The unsuitability of some algal diets for arthropods

Not all algae are eaten and utilized by arthropods. Suspension-feeding crustaceans show distinctly greater utilization of certain (usually smaller) algal cells (JÖRGENSEN, 1966), dependent on the mesh size of their filtering appendages. Therefore their feeding cannot be regarded as a process dependent only on food availability. ZARNECKI (1968) states that copepods select their diatom food from inorganic particles by some sensory perception. Other factors, pertaining to the digestibility of the algae, are also involved. Some, like *Chlorella* and *Stichococcus*, have thick cell walls which may make their contents unavailable to some of the feeders. No suspension feeder is known to utilize *Stichococcus*

(JÖRGENSEN, 1966), and its cells survive ingestion and passage through the alimentary system of the brine shrimp *Artemia,* occurring in the animal's fecal pellets (GIBOR, 1956). HUTCHINSON (1967) suggests that spinous algae, like *Rhaphidium,* may prove injurious to zooplankton feeding on them. PROVASOLI *et al.* (1959) report that whereas *Scenedesmus spinosus* is an excellent food for *Daphnia, S. oahuensis* and *S. quadricauda* are mediocre or poor foods, and offer similar observations on two *Cosmarium* species. The high iodine content of *Phyllophora nervosa* was believed by GAEVSKAYA (1958) to protect this alga from isopod grazing, though the plant constitutes 95 percent of the biomass of benthic algae at the site studied, in the Black Sea. The unsuitability of blue-green algae to planktonic grazers (BROOKS, 1969), has already been referred to (section 2. 5).

2. 10 *Arthropod feeding on dead or old algal cells*

Arthropods may subsist not only on live algae, but also on their dead and/or decomposing cells. OTSUKI, HANYA and YAMAGISHI (1969) maintained *Daphnia* on *Scenedesmus* cells which had been freeze-dried and decomposed by bacteria for several months, development of the *Daphnia* being only slightly less than on freshly-killed algal cells. From these results (and from others which they quote), OTSUKI *et al.* (*l. c.*) concluded that algal cell residues decomposed by bacteria can sustain *Daphnia* to a certain extent, growth being due to the algal residues, not to the bacterial mass. Similar results in regard to the copepod *Tigriopus* were obtained by GILAT (1967). On the other hand, STROSS, UNGER, JONES and VAIL (1965) reported that old *Chlamydomonas* cells inhibited the population increase of *Daphnia,* and RYTHER (1954) thought that old cultures of *Chlorella vulgaris* had adverse effects on *Daphnia magna.*

2. 11 *Arthropod feeding on algae in sewage beds*

Various aquatic insects which feed on algae were shown by USINGER and KELLEN (1955) to play an interesting role in sewage oxidation ponds. The algae present in such ponds can be both beneficial and harmful. By releasing oxygen during the day, the algae greatly contribute to the oxygenation process proceeding in the ponds, as the availability of oxygen is the foremost single factor in that biological system. On the other hand, old and senescent algae settle out of the water and adhere to bottom surfaces. This dead algal matter opposes the basic function of the entire purification process, hindering the operation of the oxygen ponds. Therefore any agency assisting in the removal of the senescent algal deposit will directly help the operation of the ponds, and the foremost group active in this respect are chironomid fly larvae. These insects, which feed on algae, occur in dense algal growths and detritus and are the most important factor in removing them. Furthermore, the feeding brings about the mixing of the algae at the mud-water interface, causing oxygen diffusion into the deeper layers, thereby extending the zone of aerobic decomposition (USINGER and KELLEN, 1955). In this case insects (mostly chironomid flies, but also some hydrophilid beetles and corixid bugs) may be said to function as biological control agents regulating algal populations. General confirmation for the above results of USINGER and KELLEN was reported by KIMERLE and ENNS (1968). BROOK (1955) also noted that insects play an important role in controlling algae in slow filter beds of waterworks. Efforts to manipulate *Daphnia* populations in order to enhance their action in water clarification ponds were reported by EHRLICH (1966).

2. 12 *Arthropods as pests of economically-important algae*

Arthropods have been known to achieve pest status when by feeding on algae or inhibiting their growth they caused economic damage. Such cases have been reported in laboratory cultures of algae, in kelp beds in the seas and in rice fields. LOOSANOFF, HANKS and GANAROS (1957) stated that the commonest difficulty in large-scale phytoplankton culturing (in open-air tanks) is invasion by phytophagous zooplankton, mainly copepods. Having once gained access to tanks in which *Chlorella* was cultured, the animals multiplied rapidly, consumed most of the algal cells and rendered the cultures worthless. Chemicals were finally used to control the copepods.

The giant kelp, *Macrocystis pyrifera,* forms large offshore beds in southern California. The upper parts of the plants are harvested and commercially processed, the annual harvest being about 100,000 wet tons (LEIGHTON, JONES and NORTH, 1966). These beds have considerably dwindled in recent years, mainly through the grazing of sea urchins (LEIGHTON *et al., l. c.*), but other marine animals have also contributed to their depletion. The appearance of dense populations of the crustaceans *Idothea resecata* and *Amphithoe humeralis,* with several hundred young animals per blade, was described by LEIGHTON *et al.* (1966). The animals brought about the complete deterioration of the upper 3 meters of the plants within 10 weeks. In China kelp (in this case, *Laminaria japonica*) is also of high economic value, and several amphipods are among its destructive pests (CHENG, 1969).

The adverse effects of such algal grazers — sea urchins and some crustaceans — on kelp production were inadvertently demonstrated through oil pollution in the seas. When such pollution occurs, most of the fauna is killed, with a resultant then-thousand-fold increase in sporophyte populations (BONEY, 1965).

The role of algae in improving soil fertility, with special reference to rice fields, was discussed, among others, by LUND (1967) and GUPTA (1966), respectively. Arthropods grazing on algae may subtract from soil fertility, and the elimination of the grazers may add to it. This was demonstrated by RAGHU and MACRAE (1967). These authors, working in the Philippines, noted that, in fields where the insecticide gamma-benzene hexachloride (commonly known as lindane) was applied to control the rice borer *Chilo*, more abundant algal growth occurred than in untreated fields. Subsequent experiments showed that lindane applications, at the recommended doses, caused a marked stimulation of growth of indigenous algae. This result was attributed to the elimination of algal-feeding « ostracods » by the insecticide applications. Very high lindane doses (10 times the recommended dosage) affected the composition of the algal populations (blue-greens became dominant), but the amount of algal tissue produced in the treated fields was still much larger. RAGHU and MACRAE (1967) believed that soil fertility may be increased by eliminating the arthropod grazers through pesticide applications. They also (*l. c.*) quote an earlier report by HIRANO, SHIRAISHI and NAKONO, who wrote that when they tried to inoculate rice paddies with nitrogen-fixing blue-green algae, the inoculum was rapidly consumed by small crustaceans, and pesticides had to be applied in order to proceed with the experiment. This brings to mind a remark made in 1931 by FRITSCH (see BROOK, 1955), who pointed out that the successful establishment of an alga, besides being influenced by chemical and physical factors, depends also on keeping the fauna at a minimum.

A different case of algal growth inhibition by crustaceans was reported by TIFFANY (1958). Ohio fish ponds were stocked with young crayfish, which kept the water nearly always turbid. As a result, only inadequate light penetration occurred, causing algal growth to be effectively hindered.

3. ARTHROPOD FEEDING ON ALGAE IN TERRESTRIAL HABITATS

The feeding of arthropods on algae has been far less studied in terrestrial habitats than in aquatic environments, possibly because this association has fewer economic implications. Some arthropods have been reported to feed on algae in terrestrial habitats (such feeding being always of the chewing type), but little is known about food preferences, amounts consumed and similar matters. On the whole, relatively fewer arthropods appear to feed on algae in terrestrial habitats than in aquatic ones. One reason may be that on land algae are only one of several groups of available green plants, whereas in aquatic habitats they are often the dominant or even the only primary producers. It should also be recalled that not all the main algal divisions have succeeded in the colonization of terrestrial habitats (FOGG, 1969). This limits the range of choice and may eliminate some arthropod grazers.

This limitation does not apply to algae washed onto or growing on sea and lake shores, where they may be grazed by littoral arthropods as well as by terrestrial ones. This grazing association will described first, followed by those pertaining to soil and epiphytic algae.

3. 1 Feeding on algae in the intertidal zone

YONGE (1949) recorded many arthropods which feed on algae in the intertidal zone, those grazers being mainly crabs, isopods and insects. The amphipods *Talitrus saltator* and *Allorchestes ptilocerus,* for instance, are known to feed on seashore algae (YONGE, 1949; GLYNN, 1965), though not exclusively. The isopod *Tylos punctatus* voraciously feeds on kelp (*Macrocystis*) which had been washed ashore, sometimes skeletonizing entire plants overnight (HAMNER, SMYTH and MULFORD, 1969). EVANS (1968) noted that on a world-wide basis, only few families of insects occupy the intertidal habitat, and recorded some of the kelp-feeding species, such as tenebrionid beetles of the genus *Phaleria.* Additional insects, e. g. grouse locusts (Tetrigidae), staphylinid beetles, tipulid fly larvae and others also feed on lakeshore or intertidal algae (GLYNN, 1965; IMMS, 1957).

Sea birds, representing a partly-marine, partly-aerial habitat, also serve as substrate for arthropods which feed on algae. DUBININ (cited by EVANS, SHEALS and MACFARLANE, 1961) found various diatoms (*Pinnularia, Stauroneis, Navicula*) in the gut of feather mites of the genus *Freyana.*

3. 2 Feeding on soil algae

The feeding of arthropods on soil algae is one of the lesser-known aspects of the ecology of these plants, grazing on them having scarcely been studied (LUND, 1967). KEVAN (1962, 1968) wrote that as algae, due to their light requirements, are mostly restricted to the soil surface, they support a surface-dwelling fauna. Some algal cells may, however, be translocated into lower soil layers by rain or earthworm action, and thus provide food for additional animals. Unicellular green algae and diatoms have in fact been collected from as far three meters below soil surface (PRESCOTT, 1969). Several soil arthropods which feed on algae, such as some millipedes, thysanurans, psocopterans and staphylinid beetles were noted by KÜHNELT (1961). The termite *Hospitalitermes* has been reported to feed on algae and lichens, the former group of plants being preferred (KALSHOVEN, 1958). WOODRING (1963) and LITTLEWOOD (1967) listed a few alga-feeding oribatid mites. The latter author offered soil algae to the mite *Camisia segnis* after it had been surface-sterilized, and found that either the animals or the food had to be contaminated before the mites fed on the algae. This result is reminiscent of data presented earlier (section 2. 8), pertaining to the unsuitability of single algal diets for some crustaceans.

The alga *Zygogonium* forms extensive mats on moist acid soil, and continuous growth of the mat results in the establishment of an aquatic environment beneath the alga (LYNN and BROCK, 1969). Such intermediate soil-freshwater environments support some arthropods, of which the brine fly, *Ephydra bruesi*, which probably feeds on *Zygogonium*, appears to be the most prominent. Algae also serve as primary producers in terrestrial polar regions. GRESSITT and SHOUP (1967), working in Antarctica, reported that prostigmatic mites often fed on algae growing on the ground or on rocks, and two mites of the prostigmatic family Tydeidae were found in large numbers on algae growing on dead penguins.

3. 3 Feeding on epiphytic algae

Arthropods feeding on epiphytic algae have received somewhat more attention. The psocid fauna which utilizes the microflora of larch bark was studied in England by BROADHEAD (1958). Several species were encountered, some preferring algae (*Pleurococcus*) and others lichens. Adults and nymphs of *Elipsocus* and *Mesopsocus* distinctly preferred algae to lichens, starving when offered only the latter diet (BROADHEAD, *l. c.*).

Many additional observations on the alga- and fungus-eating species of *Mesopsocus* were later published by BROADHEAD and WAPSHERE (1966). Other arthropods feeding on epiphytic algae were discussed by ELTON (1966). The tenebrionid beetle *Cylindronotus laevioctostriatus* climbs tree trunks in summer and feeds at night on the *Pleurococcus* growing there. Plecopterans of the genus *Nemoura* feed on algae and lichens growing on fallen twigs, such food being required for egg ripening. The woodlouse *Porcellio scaber* moves up and down tree trunks during the year; it lives on *Pleurococcus*, upon which it feeds at night. Summer overgrazing at lower tree levels was believed to be the reason for *Porcellio* climbing the trees, as at higher levels the alga remains abundant. Millipedes are also believed to browse on *Pleurococcus* (ELTON, 1966). It was postulated by SUSKI (1967) that tarsonemid mites of the genus *Daidalotarsonemus* feed on epiphytic algae and lichens.

4. UTILIZATION OF ALGAE BY ARTHROPODS (EXCEPT AS FOOD)

4. 1 Case and tube construction

Algae are utilized by arthropods for other purposes besides food. Chironomid larvae which feed on algae construct their larval cases from algal fragments. EDGAR and MEADOWS (1969) reported that *Chironomus riparius* larval cases may be built from mud or from a mud-algae mixture, the better-built and more quickly constructed cases being those made exclusively from algal matter (see also DARBY, 1962). BARNES (1963) mentions a shrimp, *Alphaeus pachychirus*, which constructs tubes from the filamentous mats of certain algae. The shrimp lies on its back and pulls the mat around itself like a cloak. By using one of its legs as a needle, and the algal filaments as threads, the shrimp then stitches the edges of the mat together.

4. 2 Camouflage and color changes

Several crustaceans camouflage themselves with seaweed fragments or mimic their algal surroundings by attaining similar coloration. Decorator crabs (like *Loxorhynchus grandis*, *Podochela hemphilli* and others) take pieces of seaweed and cement them on to the surfaces of their bodies and legs so that they resemble their surroundings (MACGINITIE and MACGINITIE, 1949). *Podochela hemphilli* also has a form of camouflage behavior, special bowing motions which simulate the action of the seaweed substrate. Many isopods (among other animals which frequent seaweeds) are able to orient themselves along the main axis of the stem or frond of the seaweed, thereby attaining some degree of camouflage (MACGINITIE and MACGINITIE, 1949). The amphipod *Pseudoprotella phasma* lives on the brown alga *Dictyota linearis* and closely resembles the habitus of the host plant in color, shape and form (ALEEM, 1969). The animal appears to occur almost exclusively on this plant, and when kept in aquaria with other algae it will sooner or later confine itself to *D. linearis*, which seems to be the normal biotope. The hermit crab *Calcinus elegans* occurs on Hawaiian intertidal shores in large shells often encrusted by the alga *Porolithon onkodes*. The pinkish-purple algal growth tends to obscure and camouflage the shell in a very effective manner (REESE, 1969). The ability of some crustaceans to change color and thereby mimic their algal substrate has been discussed by various authors. Isopods are well known in this respect, being green, brown or red (and even motled, on coralline algae) according to the inhabited seaweed (MACGINITIE and MACGINITIE, 1949).

The adaptive advantages which the ability to change color according to substrate confers upon the marine isopod *Idothea montereyensis* were discussed by LEE (1966). *Idothea* was found to occur in three distinct color varieties, which matched the color of the marine plants on which the animals were found. The green and brown forms of the isopod occur on living or dying (respectively) eelgrass (*Phyllospadix scouleri*), whereas the red animals are found on sheltered red algae, such as *Gigartina cristata*, *Farlowia mollis* and others. Animal coloring is modified by chromatophore action in response to food-plant coloration, and is not directly affected by the pigments present in the various plants. According to LEE (*l. c.*), there is a massive exchange of individuals between eelgrass and the red algae. Young isopods, being incapable of holding on to the exposed eelgrass (which is subject to severe wave action during winter), are swept to inshore, well-protected red algal beds. These isopods change their color to red within a week or so, and grow to maturity on the algae. At this period, increased population pressure causes many adults to migrate back to the eelgrass, where they have ample food and space, and where their color changes to green (or brown). The ability of the animals to change their coloration within a relatively short time thus permits them to exploit more plants in their habitats with greater safety from predators (LEE, 1966).

Other crustaceans are also capable of such color changes. The chameleon prawn, *Hippolyte varians,* changes its color from red to green, depending on the kind of seaweed it inhabits (YONGE, 1949). The crab *Huenia proteus* has the green color of the seaweed (*Halimeda*) on which it lives, as well as having its body shaped like part of this calcareous alga (GREEN, 1963). Some striking color photographs of the Sargassum shrimp and crab (see below for a discussion of this association), which demonstrate the degree of protective coloration attained by these animals, were presented by BERRILL (1966).

4. 3 *Substrate and shelter*

Algae provide shelter and a physical substrate for many terrestrial and aquatic arthropods. « Remove the seaweeds and a great proportion of the animal life would be swept away or die from exposure » wrote YONGE (1949). EVANS (1969) remarked that in general the intertidal insect fauna of Californian beaches is more extensive than that of the Mexican western coast, probably due to the presence of more abundant intertidal algae and subtidal kelp in the former region. Algal mats enable collembolans to colonize bare peat (HALE, 1963). Usually this habitat is impenetrable to Collembola because it cannot afford them sufficient protection from adverse climatic conditions. However, when algal mats are formed on bare peat and partially flaked away in summer, large collembolan colonies become established underneath the mats, where high humidities are maintained (HALE, 1963). The occurrence of some arthropods in Antarctic algae (GRESSITT and SHOUP, 1967) has already been mentioned. GRESSITT (1967) also reported that the prostigmatic mite *Nanorchestes antarcticus* was abundant in green and red algae growing on snow, thus being regarded as an occupier of green and red snow habitats. Barnacles and dead coralline algae (*Lithothamnium lamellatum*) form a porous, crusty mass over rocks, a microhabitat which shelters and supports some intertidal beetles (EVANS, 1968 — see also GLYNN, 1965). The larvae of some midges are reported to burrow in mats of blue-green algae and pupate there (NEEL, 1968) and juvenile stages of copepods are known to live similarly in red and brown algae (GREEN, 1963). The copepod *Macrosetella gracilis* has a creeping larva which depends on the alga *Trichodesmium thiebautii* for development in the plankton (CALEF and GRICE, 1966). Many mayflies, midges and other aquatic insects utilize algae as shelter in streams (NEEL, 1968). The trichopterans *Cheumatopsyche* and *Hydroptila* attach their pupal cases to various algae (mainly *Lemanea*) (NEEL, *l. c.*), and barnacles utilize kelp as a substrate for attachment (BERRILL, 1966). DUMBLETON (1969) reported that felted mats of blue-green algae floating on water from a hot spring in New Zealand served as ovipositing sites for an ephydrid fly, its larvae being active at temperatures as high as 51.5° C. KIMERLE and ENNS (1968) noted that floating algal mats become ovipositing and breeding sites for many groups of flies and for mosquitoes. DARBY (1962) reported that the blue-green alga *Gloeotrichia* served as substrate for chironomid larvae (which do not feed on this plant) only as long as the gelatinous bladder-like structures of the alga were firm. When the *Gloeotrichia* colonies began to deteriorate and break up, no larvae were found on them. The astigmatic mite *Hyadesia fusca* occurs only within tubes of the alga *Enteromorpha* on which it also feeds (GANNING, 1970).

An instance of crustaceans frequenting seaweed was given in the quotation at the head of this paper. And HEYERDAHL (1950) and his crew, floating across the Pacific on the *Kon Tiki*, noted that seaweeds grew attached to their balsam raft, and that these seaweed clusters were a refuge for some stowaway crabs.

5. UTILIZATION OF ARTHROPODS BY ALGAE

5. 1 Nutrient regeneration

BARLOW and BISHOP (1965) have reviewed the literature on phosphate regeneration by zooplankton. They concluded that the animals (mainly cladocerans and copepods) supply enough to satisfy the requirements of the phytoplankton in the lake they studied. HAERTEL, OSTERBERG, CURL and PARK (1969) and MARTIN (1965, 1968) found that not only may the zooplankton (mostly various copepods in all studies) regenerate the phosphate necessary for the phytoplankton, but it may also be a major source of regenerated nitrogen compounds. WEBB and JOHANNES (1969) discussed the idea that marine crustaceans release dissolved amino acids into the sea. FREY (1969) stated that *Daphnia* and midge larvae aid in the process of silica recycling because they fragment diatom frustules by their feeding activities. The plant-grazer relationship between phytophagous copepods and phototropic algae was believed by CUSHING and VUCETIC (1963) to generate the organic nutrients necessary for continuous algal production.

5. 2 *Hosts and substrates*

Various marine and freshwater algae are known to grow on arthropods, usually without causing them any direct harm (parasitic algae will be discussed in section 6. 6). FEE and DRUM (1965) collected 49 diatom taxa (in 15 genera) epizoic on the parasitic copepod *Lernaea*. The dominant diatoms were *Gomphonema* spp., which secret some gelatinous material in the form of hollow stalks, these stalks serving in turn as substrates for many other diatom species. Although the algae sometimes form a thick layer on the copepod, no evidence was obtained that this epizoic growth was detrimental to the animals in any way.

Algae of widely-separated genera, such as *Colacium* (an euglenoid) and *Chlorangium* (Volvocales) are commonly found on the backs or appendages of various microcrustaceans (PRESCOTT, 1969). Members of the former genus attach themselves to their hosts by means of a gelatinous stalk. As the infection develops, it results in plumes of *Colacium* growing on the heads and antennae of the infected copepods and insect larvae in their aquatic habitats. Several additional epizoic algae were discussed by PRESCOTT (*l. c.*) and by BOURRELLY (1959), among them members of the genus *Characium*, which appear to be confined to aquatic arthropods. Among the infected insects are several species of the culicid genus *Anopheles*, observed in Lower Bengal to support dense growths of a *Characium* often accompanied by an *Oedogonium* (IYENGAR and IYENGAR, 1932). The *Characium* (described in that paper as *C. anophelesi*) occupied most dorsal and ventral parts of the insects' bodies. Freedom of larval movement was hampered to a certain degree by the algae, which did not otherwise appear to affect their hosts. Other local insect larvae did not serve as substrates for *Characium*, and IYENGAR and IYENGAR (*l. c.*) believed *Anopheles* to be the preferred host. Additional instances of *Characium* growing on aquatic arthropods were listed in the same paper. NADSON (1928) has called attention to algae which live on various calcified animals (among them barnacles) and burrow in their shells, and the direct effect of *Fucus* growth on barnacles was discussed by BARNES and TOPINKA (1969).

Some algae, like the *Characium* noted above and several Trentepohliaceae discussed below, appear to have an affinity for arthropods as substrates. In other cases sufficient or almost continuous illumination may facilitate the growth of algae on aquatic arthropods. GLYNN (1970) observed that algae grew on marine isopods exposed to direct sunlight whereas animals provided with shelter remained essentially free of such growth. The present writer has noted that crabs kept in almost-continuously illuminated aquaria are sometimes covered by algal growth.

Algae are known to grow on terrestrial arthropods also. MAA (in GRESSITT, SEDLACEK and SZENT-IVANY, 1965) reported on an alga-bearing geometrid moth larva which occurs in moss forests in south-east China. Beetles of the genus *Gymnopholus* (especially of the subgenus *Symbiopholus*), collected in New Guinea moss forests, harbor various plants, such as algae, fungi, lichens, mosses and ferns on their backs (GRESSITT, SAMUELSON and VITT, 1968). The algae belong to several families, among them Trentepohliaceae. This plant growth was believed to serve as protection by camouflage from natural enemies, and therefore GRESSITT et *al.* (*l. c.*) called it « epizoic symbiosis ». The effect of the growth is thus similar to that attained by the decorator crabs already discussed, which camouflage their bodies with pieces of seaweed. It is of interest to note that growth of Trentepohliaceae was also observed on wings of the desert locust in India (RAMCHANDRA RAO, 1960) and on a spider in Queensland (CRIBB, 1964). Algal growths were observed by KEVAN (personal communication, 1970) on tropical and other grouse locusts (Tetrigidae) and on some New Guinea pyrgomorphid grasshoppers.

Benefits accruing to the arthropod hosts from their algal overgrowth have been described in an instance reported by WILLIAMS (1947). The host was the mole crab, *Emerita talpoida,* and the alga was *Enteromorpha flexuosa.* This association appeared to have some selective advantages for the crabs, as specimens covered by algae were much larger than the other crabs. Nutritional factors may have been the reason for this size difference, as the alga-covered crabs were believed to have a richer supply of plankton available to them (WILLIAMS, 1947). Alternatively, they could have been older individuals. As in the cases already discussed, the alga may also serve the host crabs as camouflage from predators.

A similar case of algal epizoic growth, which attracts prey to the substrate animals, has been reported in regard to the alligator snapping turtle, *Macrochelys temmincki* (NEILL and ALLEN, 1954). The carpace of the turtles is covered by a dense growth of filamentous algae, which support a large crustacean fauna, including cladocerans, copepods, ostracods and amphipods (NEILL and ALLEN, *l. c.*).

Schwimmer and Schwimmer (1968) state that the first isolation of algae in normal animal alimentary tract was made by Valentin in 1836, who found *Hygrocrocis intestinalis* in the intestine of the cockroach *Blatta orientalis*. The relevant organism is now known as *Arthromitus intestinalis*, a bacterium belonging to the order Caryophanales, class Schizomycetes (Roth and Willis, 1960), and thus outside the scope of the present review.

5. 3 Mutualism and symbiosis

A more intimate association between arthropods and an alga was described by Brock (1960), who reported on a special, apparently unique, association between *Nostoc* and two tendipedid (= chironomid) larvae, an association which benefits all partners and is therefore considered to be mutualistic. The larvae — two species of *Cricotopus* — are exclusively found in *Nostoc* pads, where they burrow, feed and pupate. The larvae are capable of reattaching the pads once these get torn from their original holdfasts; all erect pads have been found to contain the insects. As the adult midges emerge, the pads disintegrate. Shelter from predators, abundant food and high humidity were considered to be the advantages gained by the insects from the association. For *Nostoc*, the benefits were believed to be the reattachment of the colony to a firm substrate, the gaining of more sunlight (through pad erection) and the creation of more reproductive filaments due to larval feeding. These filaments are liberated as the colony is destroyed during adult emergence, thereby adding another advantage for the alga.

The occurrence of an endozoic symbiotic alga in the caudal lamellae of damsel-fly (Odonata) naiads was reported by Selvaraj and Job (1965). The alga — the colonial *Chlorosarcina* — lives both on the outer surface of the lamellae and inside them. As the algae occurred on the main tracheal branches of the lamellae, some close, respiratory relationship was postulated to exist between the insect and *Chlorosarcina*. Similarly, a *Euglena* was recently found to be endosymbiotic (on a strictly seasonal basis) with the naiads of three damsel-fly species (Willey, Bowen and Durban, 1970), but these cases appear to be extremely rare. It is of interest, and the point will be further discussed below (section 9. 1), that neither Buchner (1965), in his treatise on endosymbiosis of animals with plant micro-organisms, nor Droop (1963) and McLaughlin and Zahl (1966), in their reviews on symbiotic algae, mention any cases of arthropod — alga symbiosis.

5. 4 *Dispersal*

Another type of relationship through which algae may benefit from their association with arthropods involves the dispersal of some algae by various pterygote insects. The subject has been reviewed by STEWART, MILLIGER and SOLON (1970), who also added many original observations. Numerous insects which spend part of their lives in or near water, whether perching, foraging or ovipositing, are capable of disseminating adherent or eaten algae. The insects include water beetles, aquatic bugs, crane flies and mosquitoes, dragonflies and damsel-flies, caddis flies and mayflies. The commonest algae carried by the insects were members of the Chlorophyta (especially *Chlorella* and *Chlorococcum*) and the Cyanophyta (especially *Phormidium*). As the same algae were found to be commonly transported by quite different insects, it is believed that there is little specificity in this insect-algae relationship (REVILL, STEWART and SCHLICHTING, 1967). An exception are the colonial Volvocales, which appear to be disseminated primarily through the alimentary tract of phytophagous species (MILLIGER, STEWART and SILVEY, 1971).

The occurrence of corixid bugs, such as *Sigara alternata* and *Ramphocorixa acuminata*, in shallow, summer-dry lakes in Texas and Mexico is of particular ecological interest. The water bugs were found to carry disseminules of many algae, suggesting that they had an important role in the annual reintroduction of algae into such lakes (STEWART *et al.*, 1970). These authors conclude by stating that this finding constitutes evidence that aquatic insects are important (though passive) transport vehicles for the algae (and Protozoa), contributing to their distribution and introduction into suitable but isolated aquatic habitats.

Terrestrial beetles were also shown by these authors (MILLIGER *et al.*, 1971) to disseminate various algae. Noteworthy in this respect are members of the family Cicindelidae, which often frequent habitats between aquatic and terrestrial environments, and thus pick up disseminules from both. WALLWORK (1967) presented the photograph of an oribatid soil mite (*Halozetes*) whose cerotegument had diatoms adhering to it. This suggests that such mites, as well as other soil animals, may assist in the dissemination of algae in the soil.

(to be continued)

THE ASSOCIATIONS OF ALGAE WITH ARTHROPODS - II *

U. GERSON **

6. DELETERIOUS EFFECTS OF ALGAE ON ARTHROPODS

6. 1 PHYSICAL INTERFERENCE

Several cases of algal growth on arthropods were noted above. Some appear to be fortuitous, others serve to camouflage the hosts, and in additional ones, to be discussed below, the algae parasitize the arthropods. The overgrowing plants may also adversely affect the host through physical interference. A pertinent report (GLYNN 1970) concerns algae growing on the marine isopod *Dynamenella perforata*, causing it indirect harm by interfering with crawling, swimming, feeding and other functions. BARNES and TOPINKA (1969) wrote that *Fucus* initially receives some protection from the barnacles on which it grows, but later the plants kill the animals by interfering with their feeding activity.

Indirect physical interference through decreasing transparency brought about by increasing phytoplankton production in lakes and rivers was postulated by FREY (1969) to affect populations of chydorid cladocerans. These animals utilize rooted aquatic plants as their main substrate, and the greater and deeper the area inhabited by the plants, the more varied the cladoceran populations. In low-productivity water bodies the plants extend to deeper zones, due to the greater transparency of the water. But with increased phytoplankton production transparency decreases, the extent of rooted aquatic plants becomes restricted, and consequently the number of cladoceran species declines.

6. 2 OXYGEN DEPLETION AND OVERPRODUCTION

The depletion of oxygen in ponds by algae, or its overabundant production there, are specific mechanisms whereby arthropod populations may be affected

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(EHRLICH 1966). *Chara fragilis* was lethal to some mosquitoes apparently due to excessive oxygen production (DARBY 1962). MARSHALL (1966) stated that *Daphnia* suffered prenatal mortality when held in a *Chlamydomonas* culture kept in the dark, possibly due to depletion of dissolved oxygen by the algae. Water trapped by large brown seaweeds (such as *Fucus* and *Ascophyllum*) at low tide becomes deficient in oxygen during the night or on cloudy days (WIESER and KANWISHER 1959). The lack of oxygen may paralyze or kill the arthropods which usually inhabit these brown algae. Efforts to reduce the amplitude of the diurnal oxygen curve in stabilization ponds so as to maintain *Daphnia* populations which help in water clarification, were detailed by EHRLICH (1966).

6. 3 INHIBITORY SUBSTANCES

SAUNDERS (1957) stated that there is some evidence for antagonistic activity of algal populations towards microcrustaceans, often enhanced by release of a substance from ingested cells within the animals. A tannin which immobilized the *Sargassum* epifauna was discovered by SIEBURTH and CONOVER (1965), the branch tips of the seaweed being observed to be virtually free of the usual epibiota. Appropriate chemical tests suggested the causal factor to be a tannin, which adversely affected copepods at dilutions up to 1 : 125, but not at higher ones (SIEBURTH and CONOVER 1965). Some other instances of this phenomenon were presented in reviews by LUCAS (1961) and SIEBURTH (1968). The term «ectocrines» was coined by LUCAS (1947) to denote biologically active excretory products of aquatic organisms that may have effects in marine ecology. A pertinent example was presented by SIEBURTH (1968). The brown alga *Ralfsia verrucosa* secretes some polyphenols which kill barnacle nauplii, thereby preventing their settlement in pools where the alga abounds.

6. 4 WATER BLOOMS AND TOXINS

The best known cases of toxin production by algae are those associated with «water blooms». The causes and development of these phenomena were discussed by LUND (1965), ROUND (1965), STRICKLAND (1965) and many others. These great outbursts of algal growth are often associated with widespread poisoning of fishes, birds, crustaceans and even terrestrial animals, which may suffer after drinking the waters (ROUND 1965). The pertinent literature was recently summarized by SCHWIMMER and SCHWIMMER (1968) (but see also VALKANOV 1964). Copepods, cladocerans, amphipods and decapods were among the affected crustaceans.

RYTHER (1954) believed that in rapidly multiplying algal populations some inhibitory substance («chlorellin») accumulates, which seems to exclude the grazers (the basis for this postulate, HARDY's exclusion theory, was discussed in a former paragraph). Later writers (RIGLER 1961; TAUB and DOLLAR

1968, and others) criticized RYTHER and did not accept his chlorellin theory. TAUB and DOLLAR (1968), for instance, explained *Daphnia* inhibition at high algal concentrations by nutrient deficiencies rather than by toxic substances. A case where an alga is poisonous to arthropods only in special circumstances was described by STANGENBERG (1968). The plant was *Microcystis aeruginosa*, which contains a toxic substance. When *Daphnia* and *Eucypris* were kept on normal cultures, no mortality occured. But the toxin may be discharged from the algal cells by refrigerating and defrosting them. Considerable copepod mortality took place when such refrigerated-and-defrosted cells were placed in the cultures.

6. 5 THE BIOLOGICAL CONTROL OF MOSQUITOES BY ALGAE

Several authors have remarked on the effect of Characeae and other algae on mosquito larvae. FRITSCH (1956, p. 447) noted the frequent avoidance of waters harboring these algae by the larvae, though there was no clear evidence for the production of any larvicidal substances by the Characeae. REMUSAT (1962) claimed to have experimental proof that the larvae disappear from Characeae-containing waters because of the algae. It is only one step from such observations to utilizing them, i. e., manipulating the algae in order to control insect pests biologically. A review of such projects was presented by FRANZ (1961), who noted that most of these efforts were against mosquito larvae. The best results were reported by GERHARDT (1953, 1955). This author noticed that rice fields free from mosquito larvae supported rich blue-green algae, whereas the pests abounded in fields with lesser algal growths. GERHARDT (*l. c.*) wrote on the algae employed, on their culture and on successful introduction experiments. The green alga *Oedogonium princeps* is another promising agent for the control of anopheline larvae (GHOSH and HATI 1964). Other species may also prove useful in this respect, and on the whole it seems that the utilization of algae against insect (and other) pests which live in aquatic environements has been rather neglected.

6. 6 PARASITISM

Several algae are parasitic on arthropods, although it may sometimes be difficult to distinguish this association from the mere utilization of the animals as substrates (discussed in section 5. 2). FRITSCH (1956) cites CHATTON's work on endoparasitic algae, including the genera *Paradinium* and *Blastodinium*. Members of the latter genus castrate their copepod hosts (SEWELL 1951) and sex reversal in an attacked animal was reported by CATTLEY (1948). Many Euglenoidina were recently described as parasites of fresh-water copepods (MICHAJLOW 1966, 1968, etc.). The parasites attack the eggs and intestines of the hosts, often causing their death. In some cases the parasites begin their development in the nauplial eye and then spread to other parts of the body (MICHAJLOW 1966).

6.7 ENTANGLEMENT

This mechanism was reported in regard to fishes, not arthropods, but it is pertinent to note it here. The water net, *Hydrodictyon reticulatum*, is a colonial alga whose cells become 4-5 mm long, forming a network with a mesh size of 6-8 mm in older plants. The colony forms a sac measuring up to 50 mm in diameter and 200 mm in length (LEWIS 1961). Many small fishes become entangled in the net, and, if unable to free themselves, they eventually die there. LEWIS (*l. c.*) thought that the alga may indirectly derive nutrients from the decaying fish, exerting a significant effect on small fish and fingerling populations. It is quite likely that some of the larger aquatic arthropods may similarly become entangled.

6.8 INDIRECT EFFECT OF HYDROLYZED SEAWEED

Some reports have been published in recent years concerning the indirect, adverse effects of algae, as hydrolyzed seaweed, on arthropods pests of agricultural crops. Some of the claims in these reports may have commercial undertones, but it seems worthwhile to note them in the present context. STEPHENSON (1966) stated that liquified seaweed, marketed as «Maxicrop» in the United Kingdom, may confer on broad beans, sugar beets and potatoes some resistance to infestation by aphids. The resistance was considered to be behavioral rather than nutritional, as the aphids (some of which are important plant virus vectors) were wandering restlessly on the plants. Maxicrop was also reported to protect orchard trees against infestation of red spider mites (Tetranychidae), almost like commercial pesticide treatments. The seaweed product appeared to have the additional advantage of continuously building up its effect, so that after 2-3 years the degree of control achieved was as good or better than that obtained by conventional acaricides. These effects were thought to be due to the enhanced effect of predators, which were unaffected by Maxicrop (STEPHENSON, *l. c.*).

The mecanisms protecting the Maxicrop-treated plants against these pests are not clear, but it is beleaved that the effect is mediated through the plants, and that it is not insecticidal (STEPHENSON 1966). Growth-regulating properties were also claimed for Maxicrop, and these may be involved in protecting the plants (BOOTH 1969).

A case of historical interest, concerning an attempt to protect potato plants from «potato bugs» with the help of algae, was related by SCHWIMMER and SCHWIMMER (1968). «Green lake scum» was applied to the potatoes, apparently to control the bugs. As a result both potato plants and bugs died.

7. ALGA-ARTHROPOD COMMUNITIES

7.1 COMMUNITIES ON SEAWEED AND ON FRESHWATER ALGAE

Certain arthropods have been associated with algae for prolonged periods, during which they formed some specific communities. One such community is attached to *Sargassum* seaweed in the Sargasso Sea. This plant, originally coming from the coasts of the Caribbean and covering large areas in the Sargasso Sea, affords the base for a nomadic fauna of littoral origin, presumably stemming from the home of the seaweed (ALLEE and SCHMIDT 1951). There are only 16 animal species directly attached to this *Sargassum*. The animals had to undergo several adaptations in order to survive on this pseudobenthos, adaptations which include specialized attachment behavior, nest building and protective coloration. There are some arthropods among them, such as the crab *Planes minutus* and the shrimps *Leander tenuicornis* and *Latreutes ensiferus* (ALLEE and SCHMIDT 1951). A note of historic interest may be inserted here again. As Columbus was crossing the Atlantic in 1492, his crew observed seaweed floating by, with a crab attached to it. This sight suggested the proximity of land to the sailors, but actually they were only about midway across the ocean, sailing through the Sargasso Sea (BERRILL 1966).

ANDREWS (1945) recognized several faciations of algae and animals inhabiting kelp beds in the sea near the coast of California. Arthropods are involved in two of these faciations, one of which consists of *Macrocystis* and the decapod *Pugettia*, and appears to be seasonal. *Nereocystis* and the amphipod *Amphithoe* make up the other faciation which is permanent throughout the year. Assemblages of algae and ostracods were distinguished by WHATLEY and WALL (1969) in the southern Irish Sea. The laminarian assemblage was exclusively found on the holdfasts of *Laminaria digitata* and *L. hyperborea*, and its dominant ostracod was *Loxoconcha rhomboidea*. The littoral assemblage was dominated by *Cythere lutea* and *Heterocythereis albomaculata*, and occured on *Cladophora, Enteromorpha* and *Corallina*, but never on *Laminaria*. A *Fucus serratus* community, which includes many alga-feeding arthropods, were postulated to exist near the Swedish coast by HAGERMAN (1966). This author also noted that the alga's surface has a pronounced effect on the associated fauna, filamentous, scrub-like algae having richer faunae than leaf-like ones. Similar observations were recorded by JANSSON (1967), WHATLEY and WALL (1969) and others.

7.2 COMMUNITIES LIVING IN SEASHORE WRACK

BACKLUND (1945) conducted an extensive study of the faunae occuring in seashore wrack on Scandinavian shores, listing many arthropods. Later literature on this subject was reviewed by STRENZKE (1963), in the introduction to his experimental study of arthropod succession in seaweeds. This investigator placed fresh *Fucus* and *Enteromorpha* in open wire baskets near the seashore, and studied the arthropods occuring therein for a period of one year. Four distinct faunistic phases, correlated with sodium chloride content, were observed. In the initial, colonizing phase, during the first fortnight of sampling, the anthomyiid fly *Fucellia intermedia* and the mesostigmatic mite *Halolaelaps marinus* predominated. Little decay occured during this phase, nor were there any significant changes in the NaCl or water content. The second, «decayed matter» phase lasted from the third week to the beginning of the fourth month, and the dominant arthropods were the spheroceriid flies *Limosina* spp. and the mite *Halolaelaps celticus*. NaCl content was still above 10%. During the third, «transitional» phase, the salt concentration fell to below 2%. This phase lasted up to 7-8 months from the experiment's beginning, and the more abundant animals were certain flies, such as the syrphid *Syritta* and the scatopsid *Scatopse*. The final phase was characterized by large numbers of the mosquito *Trichocera* and the collembolan *Hypogastrura*. Water content was believed to have an important modifying effect on this succession (which could be replicated during several years), but the dominant factor was considered to be sodium chloride content.

Additional work along the same lines has more recently been reported by MOELLER (1967), who found that Collembola, which tend to avoid high salinity conditions, have no effect on algal decomposition. YONGE (1949) considered the seaweeds to represent a «factor of the first importance» in the lives of many shore animals (arthropods included). Other observations on intertidal, kelp-utilizing insects were recorded by EVANS (1968), who also summed up many of the previous reports. One group which deserves special mention is the dipterous family Coelopidae, the seaweed or kept flies. These insects, occuring the year round in seashore wrack, spend their entire lives therein, as it provides them with a warm, humid environment and with the nourishing slime upon which the larvae feed (OLDROYD 1964).

The possible significance of seaweed banks as sites where the transition of animals from aquatic to terrestrial habitats could take place was discussed by LAWRENCE (1953). This author studies the cryptic soil arthropods of South African forests and noted that many of these animals had relatives able to live in the littoral. He believes that many archaic arthropods, in their attempts to live on land, initially colonized the intertidal zone where heaps of seawrack could afford them temporary shelter. Thus LAWRENCE (*l. c.*) thinks that seaweed beds, with their perpetually-moist interiors, might serve as terrestrial outposts for the colonizing arthropods eventually destined to live in forest soil. This theory was also discussed by KUEHNELT (1961), who did not however accept it.

7.3 COMPETITION FOR SETTLING SITES

Intertidal zones are sometimes the scene of competition for settling sites between arthropods (such as barnacles) and algae. A universal system of zonation for the area between tide-marks on rocky coasts was introduced by STEPHENSON and STEPHENSON (1949), who designated the middle part of the shore as the Balanoid zone. Various algae, among them fucoids, are known to interfere with the barnacles there. One such scene was described by RIGG and MILLER (1949) from the vicinity of Neah Bay, Washington, U.S.A. The animals were usually more successful in occupying the available sites, often completely crowding out the algae to the very borders of the barnacle colonies. In other areas algae gained additional anchorage by pushing their holdfasts among the animals. On the other hand, the latter were sometimes restricted to narrow belts above the algal beds, as the plants were apparently better adapted to the immediatly-adjacent vertical ranges (RIGG and MILLER 1949).

Germlings of *Fucus vesiculosus* attach onto barnacles and clams better than onto rocks, but their holdfasts are also easier to detach from the former surface. *Fucus* subsequently kills the barnacle on which it grows, and the empty shell with its algal growth is devoured by grazing limpets. These interactions were shown by BARNES and TOPINKA (1969) to affect the competition for space between barnacles and algae.

In exposed areas *Fucus* is less abundant than barnacles, as the alga often detached by wave action before attaining a size sufficient to kill the animals. With decreasing exposure the algae succeed in developing bigger plants, subsequently killing the barnacles (which are then removed by limpets). As a result the sheltered areas become available for further colonization by the algae, which grow on other substrates and deny access to invading barnacles. Additional observations on this subject were reported by MACFARLANE (1952) and GLYNE (1965) published an extensive study on algal-barnacle relationships and communities. Competition between algae and other arthropods - simuliid larvae - for space on rocks was reported by FEE (1967).

7.4 COMMUNITIES AFFECTED BY TECHNOLOGICAL CHANGES

Modern technology is bringing about many changes in algal distribution and abundance (and presumably in their associated arthropod fauna), and some representative cases will be noted. The hulls of present-day fuel tankers are generally free of animal fouling forms, apparently because of the ships' fast movement from tropical, warm seas to temperate waters. While this wide range of environemental conditions largely excludes animal foulers, it is highly favorable to certain algae, especially *Enteromorpha* (EVANS and CHRISTIE 1970). It may be predicted that this fouling alga, currently invading a new habitat, will eventually be found to have its own characteristic associated arthropod fauna on the tankers' hulls.

Lake Kariba in Central Africa is an artificial lake created in 1958 by damming the Zambezi River. Submerged trees serve as a newly-created substrate for animals (including arthropods) in this lake. The richest faunal standing crop was found where benthic algal populations were well developped (McLACHLAN 1970). In this case alga-arthropod communities are also evolving on a new and artificial substrate, but probably in the pattern they follow elsewhere.

Another example pertains to terrestrial epiphytic algae. ELTON (1966) noted that *Pleurococcus viridis* appears to be relatively resistant to industrial soot pollution in England, thus sometimes remaining the dominant epiphyte on tree trunks. Many arthropods depend on various epiphytic algae and lichens for food (BROADHEAD 1958; ELTON 1966). The relatively recent dominance of *Pleurococcus* will either exclude the animals which cannot utilize this alga, or make them change their diet.

The effects of pollution and its often resulting eutrophication of waterways and lakes on algae and their grazers have been discussed by various authors; a useful summary was presented by BROOKS (1969).

7. 5 SOME GEOLOGICAL ASPECTS OF ALGA-ARTHROPOD ASSOCIATIONS

The frequent concomitant occurence of algae and arthropods in fossil beds attests to their manifold associations in the geological past. Algae have an affinity for silica, transforming it to the colloidal state, in which animals may be trapped. The resulting fossils are silicified arthropods which occur in calcareous lakebed nodules (PIERCE 1961).

The evolution of animals which feed on and burrow in algae was believed by GARRETT (1970) to have caused the decline of stromatolites. These are laminated structures built by dense mats of blue-green algae which selectively trap and bind sediment particles among their mucilaginous filaments. Stromatolites abounded in the Precambrian and declined from the Ordovician to become scarce in the Cenozoic. GARRETT (*l. c.*) suggests that this decline can probably be correlated with the evolution of new grazing and burrowing animals which began to appear during the Ordovician expansion. Further, the available geological data indicate that stromatolites and animals are usually mutually exclusive. To support his arguments, GARETT (*l. c.*) presents evidence that grazing and burrowing animals (gastropods, polychaetes, fishes and some arthropods such as shrimps and crabs) may prevent the formation of mats of blue-greens and destroy algal laminations.

Past periods of increasing phytoplankton production and lake eutrophication were deduced by FREY (1964) from changes in cladocerans occuring in Quaternary sediments. *Bosmina longirostris* is considered to be characteristic of more productive situations, and its replacing *B. coregoni* is thus considered evidence for increasing productivity in the water bodies whose sediments were studied. Although FREY later (1969) expressed some reservations about his interpretations, the method still appears to be rather suitable for similar reconstructions. Such an effort was made by SEBESTYEN (1969), who postulated past changes in the water level of Lake Balaton (Hungary) from the relative abundance of the alga *Pediastrum* and of cladoceran remains in lake sediments. As the alga is believed to be planktonic, its greater abundance (relative to Cladocera) indicates past periods during which a high water level persisted, with a corresponding dominance of planktonic life. The relative dominance of the Cladocera in the sediments, on the other hand, would suggest decreased water level periods during which benthic life was more abundant.

Past associations between arthropods and algae may have some bearing on the origins of oil, as discussed in section 2. 4. A different link was suggested by IOVINO and BRADLEY (1969). These authors found that the ooze in Mud Lake, Florida, consists exclusively of minute faecal pellets produced by larvae of the fly *Chironomus* whilst feeding on blue-green algae. The resultant pelletal ooze appears to be similar to lacustrine organic ooze believed to be the precursor of rich oil shale beds in North America. The analogy between the lacustrine copropel of Mud Lake and Eocene oil shale precursors is enhanced by the discovery of minute faecal pellets in thin sections of oil shale, and of immature chironomid remains in rich oil shale beds.

8. EFFECT OF PESTICIDES

8.1 EFFECT OF ALGICIDES ON ARTHROPODS

Many herbicides are currently being used to control algae in various habitats (MULLIGAN 1969). Copper sulfate, among the better known and more widely used compounds, is toxic to *Daphnia* and other aquatic arthropods (FISHER 1956; ROSE 1954). The toxicity of various aquatic herbicides to *Daphnia* was avaluated by CROSBY and TUCKER (1966), who concluded that several of these compounds may present a hazard to various major organisms in the food chain.

8.2 EFFECT OF INSECTICIDES ON ALGAE

Insecticides may reach the algae in their aquatic or terrestrial habitats both intentionally an unintentionally. In the former case, the chemicals are applied directly, to control arthropods grazing on algae (RAGHU and MACRAE 1967), crustacean parasites of commercial fish (LAHAV and SARIG 1967) or flies breeding in washed-up seaweeds (MARX 1967). Unintentionally, insecticides reach algae through runoff or drift from treated areas. The various responses of different algae to insecticides were discussed by several authors. MENZEL, ANDERSON and RANDTKE (1970) showed that three chlorinated-hydrocarbon pesticides vary greatly in their effects on four species of marine algae. The most sensitive of these, *Cyclotella nana*, was inhibited in its photosynthetic activity and in its growth by concentrations as low as 0.1 - 1.0 parts per billion. *Dunaliella tertiolecta*, on the other hand, was completely insensitive, and the other two species were intermediate in this respect. The possibility that the differential effect of pesticides may affect the succession and dominance of certain algae was also discussed by MENZEL *et al.* (1970). Additional insecticides were similarly tested by MOORE and DORWARD (1968), who also found that various algae were differently affected by these chemicals. Malathion, an important organophosphorous insecticide, was quickly metabolized by some algae, a finding which led to the conclusion that these plants may be important factors contributing to the disappearance of pesticides from natural communities. The use of algae as pesticide indicators was advocated by MOORE (1967), though CHOLNOKY-PFANNKUCHE (1969) warned against generalizations obtained from bioessay tests with these plants.

Some algae which may be quite resistant to insecticides appear capable of biologically concentrating these compounds in their bodies (VANCE and DRUMMONS 1969). The crustacean suspension feeders, in their turn, also concentrate such substances from their algal food, and may thus ingest and accumulate high insecticide doses. Generally, the aquatic arthropods are far less insecticide-resistant than are the algae. The danger of such poisoning and its effect on the food chains in the oceans was noted by MARX (1967).

9. DISCUSSION

9. 1 THE SCARCITY OF SYMBIOSIS

Apparently the only arthropods so far reported to have symbiotic or mutualistic associations with algae are damsel fly naiads (SELVARAJ and JOB 1965; WILLEY *et al.* 1970) and chironomid larvae (BROCK 1960). One thus becomes aware of what is perhaps the outstanding feature of the associations between algae and arthropods, namely, the extreme scarcity of symbiosis between these two groups of organisms. Both groups have many times evolved symbiotic relationships with representatives of other phyla. The insects (to mention the dominant arthropod class) have bacteria, yeasts and fungi as their plant symbionts (BUCHNER 1965). Various symbiotic alage have Protozoa, Porifera, Coelenterata, Ctenophora, Rotatoria, Platyhelminthes, Annelida, Mollusca, Echinodermata and Tunicata as their animal hosts (DROOP 1963; McLAUGHLIN and ZAHL 1966). No arthropod host for algae was listed by any of these authors, nor has a symbiotic alga been recorded as present within an arthropod host by BUCHNER (1965).

Though one is at a loss to explain the rareness of symbiotic relationships between algae and arthropods, several ideas come to mind. The foremost is that so few of these associations have been recorded simply because they have not yet been discovered. McLAUGHLIN and ZAHL (1966) noted that additional alga-bearing animals are constantly being reported. Further, as DROOP (1963) remarked, tropical animals, which have higher rates of metabolism than their temperate-zone counterparts, may have a greater need for the complementary services of symbiotic algae. It is just these tropical arthropods which are the less known, and it is among them that additional symbiotic relationships with algae may be found. The recent reported instances of arthropod-algal symbiosis (SELVARAJ and JOB 1965; WILLEY *et al.* 1970) lend support to the argument that many symbiotic associations remain undiscovered.

Another possibility is that algal symbiosis has, in fact, evolved in some arthropods, but as these became extinct, the relationship died out.

DROOP (1963) noted that, despite the occurence of algal symbiosis in animals representing many phyla, few algal types participate in these associations, the commonest being zoochlorellae of the genus *Chlorella*. This suggested to DROOP (*l. c.*) that few algae are sufficiently tolerant to their hosts to be able to live within them. The lack of enough algal candidates for symbiosis may thus contribute to their scarcity in arthropods. And even algae capable of such associations may require a change in host resistance through some weakness in order to become established. A recent case of human algal infection is pertinent in this respect. KLINTWORTH, FETTER and NIELSEN (1968) reported on a case of human cutaneous infection caused by *Prototheca wickerhamii*, an achloric alga which sometimes occurs saprophytically on animals and men. The patient, suffering from diabetes mellitus and breast cancer, was under heavy drug treatment. To explain the pathogenic occurence of *Prototheca*, KLINTWORTH *et al.* (*l. c.*) postulated that both the disease and the drugs altered and lowered body resistance, thus enabling the alga to become cutaneously established. It is of interest to note that *Prototheca* «appears to be no more than a colorless *Chlorella*» (FRITSCH 1956), the commonest symbiotic zoochlorella.

A different factor contributing to the scarcity of algal-arthropod symbiosis may be the production of inhibitory substances by the algae : see reviews by LUCAS (1961) and SIEBURTH (1968). It is noteworthy that some coral zooxanthellae produce terpenes which inhibit and exclude other animals (McLAUGHLIN and ZAHL 1966).

Whatever the validity of these speculations (and admitting that they do nothing to explain symbiosis between algae and other animals), the scarcity of algal-arthropod symbiosis remains an unexplained biological phenomenon.

9.2 A PROPOSAL FOR ALGAL MANAGEMENT

This survey of algal-arthropod associations has shown that algae may be both beneficial and harmful . They are involved in sewage treatment and enrich the soil with nitrogen, they form the base of the great food chains in the oceans (and some fish ponds) and are utilized for many commercial purposes. On the other hand, algae cause «water blooms» that are sometimes toxic, and the «decay» of water bodies (FERGUSON 1968); they are weeds in kelp beds (CHENG 1969) and even pests of woody plant cuttings (COORTS and SORENSON 1968) and tea and coffee crops (FRITSCH 1956). For a detailed «algal ledger», presenting the credits and debits of algae, see PRESCOTT (1969).

The above presentation is intended to convey the idea that a greater effort should perhaps be made to manipulate algal populations. The harm algae do may be reduced or, conversely, their beneficial effects can be enhanced. The potential of algae as biological control factors has hardly been tapped, and the possibility of biologically suppressing algal pests is still only a suggestion (MULLIGAN 1969). Such manipulation obviously calls for an interdisciplinary attack on algal ecology (SIEBURTH 1968), for better management of algal resources or, to use a term currently in vogue, for algal management. (The term was recently introduced in a more restricted sense by MULLIGAN 1969). Evidently the preservation and manipulation of algal resources is to be but part of the preservation of all marine and freshwater resources, as advocated by various authors (i. e., MARX 1967). However, because of the dual potential of algae, their ability to be both beneficial and harmful, some special measures are needed, and hence this proposal for algal management.

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THE ASSOCIATIONS OF ALGAE WITH ARTHROPODS

ADDENDUM

U. GERSON

Many additional papers and books which discuss various aspects of the associations between algae and arthropods have become available since the preparation of this article. Only the more relevant ones will be noted, arranged under the same section headings and in the same order.

1. INTRODUCTION

A review on the associations between lichens and arthropods was prepared and published (GERSON 1973) whilst awaiting publication of the present paper.

2. 2 SEASONAL, DIURNAL AND STAGE-DEPENDENT FEEDING

DEONIER (1972) reviewed the algophagus habits of adult shore flies (family Ephydridae). These flies use their prestomal teeth to scrape algae off the substrates, leaving depressions in the algal mats.

JOSEPH (1974) reported on the effect of tidal rhythm on the feeding activity of *Hyale hawaiensis*. This intertidal amphipod feeds on the green alga *Enteromorpha compressa*, feeding being most intense at high tide, as the algal belt becomes covered by rising water. Ebb entails decreased feeding. This rhythmic phenomenon is believed (JOSEPH, *l. c.*) to be caused by the inhibitive effect of depleted oxygen caused by algal respiration.

2. 3 ALGA-ARTHROPOD FOOD CHAINS

The book «Marine Food Chains», edited by STEELS (1970), contains some relevant papers on marine arthropods. CUMMINS (1973), in his review on trophic relations of aquatic insects, notes various alga-feeding species.

2. 5 PHYTOPLANKTON-ZOOPLANKTON INTERACTIONS

ESAIAS and CURL (1972) conducted grazing experiments with 3 species of bioluminescent dinoflagellates and 3 calanoids. Ingestion rates were lowest for the highly bioluminescent dinoflagellates. The authors attach considerable survival value to the dinoflagellates' flashes of light, postulating that these flashes serve to defend their emitters by startling and confusing copepod grazers. ESAIAS and CURL (*l. c.*) further believe that this bioluminescence, by causing selective feeding, could be a factor in the formation of red tides and permanent blooms of biolumenescent dinoflagellates.

2. 8 REARING ARTHROPODS ON ALGAE UNDER CONTROLLED CONDITIONS

Various laboratory studies have recently been published on the effects of diverse algal diets on aquatic arthropods (ARNOLD 1971; BATTAGLIA 1970; BETOUHIM-EL and KAHAN 1972; NASSOGNE 1970; SCHINDLER 1971, and others). The results of these studies support the opinion that increasing the number of algal species in culture media enhances the survival rate of more arthropods species. This is due to the considerable selectivity exercised by the arthropods (mainly copepods) in regard to the species of algae available, their size and concentration. SCHINDLER (1971) expressed the opinion that phytoplankton-zooplankton correlations, often used to show relationships, are deficient whithout a better understanding of feeding relationships between algae and their grazers.

2. 9 THE UNSUITABILITY OF SOME ALGAL DIETS FOR ARTHROPODS

The algae *Anacystis nidulans, Merismopedia* sp. and *Synechocytis* sp. showed some toxicity or inhibition toward *Daphnia pulex* when offered as food (ARNOLD 1971). *Calanus helgolandicus* releases most of its daily captured ration of the diatom *Biddulphia* as undigested foodstuff (CORNER, HEAD and KILVINGTON 1972). The reason is not known; explanations offered include difficulties in diatom cell assimilation or possible inhibitory substances present therein. Best growth rates of the harpacticoid copepod *Euterpina acutifrons* were obtained with algal cells of medium size (7-16 μm) (NASSOGNE 1970). Smaller (6-7 μm) or wider ($>$ 16 μm) algae gave lower rates or did not support adult survival; algal food size may therefore be a limiting factor for these arthropods. Somewhat similar observations were reported by WINTERBOURNE (1971) in regard to larvae of the caddisfly *Banksiola crotchi*. They feed on stripes which they scrape from filamentous algae. As these larvae cannot digest unbrocken algal cells, algae with broad and long cells constitute the food best utilized; stripes from such algae have the highest ratio of brocken to unbrocken cells. On the other hand, algae with small cuboidal cells, such as *Hyalotheca*, constitute inefficient diets (WINTERBOURNE 1971).

PORTER (1973) conducted experiments on differential grazing by crustacean zooplankton on a natural phytoplankton community in Fuller Pond, Connecticut, U.S.A.. From her results PORTER (1973) concluded that, by their response to grazing, algae can be divided into three major groupings that cut across taxonomic lines. One group contains large, rare or filamentous species which are either unavailable to the grazers or actively rejected. Algae in the second group are small and edible, while those in the third are encased in thick gelatinous sheaths. Such algae pass intact through the alimentary system of their grazers, coming out in viable condition. Consequently, algae in the first group remain unaffected by such grazers, those in the second decrease in numbers, and species in the third group increase (through fragmentation and competitor suppression).

Data on the protection afforded bioluminescent dinoflagellates against copepod grazers (ESAIAS and CURL 1972) were noted in the addendum to section 2. 5.

2. 12 ARTHROPODS AS PESTS OF ECONOMICALLY-IMPORTANT ALGAE

The periodical Nova Hedwigia has devoted its Heft 32 to «The biology of Giant Kelp Beds (*Macrocystis*) in California», edited by W. J. NORTH (1971). t contains several papers on kelp grazers, including arthropods.

The manipulation of arthropods for the biological control of some seawed pests was suggested by MANN (1973). Sea urchins (*Strongylocentrotus* spp.) graze heavily on seaweed and kelp in many parts of the world. MANN (*l. c.*) postulated that recent sea urchin outbreaks were triggered by reductions in the populations of their predators. The lobster *Homarus americanus* is considered to be the key sea urchin predator in eastern Canada. Its numbers were seriously reduced through human activity, and MANN (1973) advocates the protection and augmentation of lobster populations for the purpose of sea urchin control.

3. 1 FEEDING ON ALGAE IN THE INTERTIDAL ZONE

The thysanuran *Petrobius brevistylis* lives in rock crevices along the beach, where it feeds on *Pleurococcus* (LARINK 1968). Grapsid crabs were reported by GRIFFIN (1971) to feed on red and green algae, which they scrape off the surface of rocks in Tasmania.

3. 2 FEEDING ON SOIL ALGAE

The collembolan *Hypogastrura viatica* feeds exclusively on unicellular algae, which are very abundant in the upper soil layers where it lives. Subsoil algae become available to *Hypogastrura* through the burrowing activities of other insects, such as beetles and fly maggots (KRAAN and VREUGDENHIL 1973). RAPOPORT and TAGLIABUE (1964) applied dried and ground littoral algae as soil fertilizer, and noted first a decrease and subsequently an increase in soil arthropod populations. The authors believe this increase to be due to the enhanced fecundity of algae-feeding arthropods as well as to attraction of outside animals to the new and abundant food source.

WHEELER, HAPP, ARAUJO and PASTEELS (1972) isolated a pygidial secretion from the staphylinid beetle *Bledius*. One or more components of this secretion may regulate the growth of algae which flourish within the burrows of *Bledius* and upon which the beetles feed.

4. 1 CASE AND TUBE CONSTRUCTION

The importance of algae in the behavioral ecology of the shrimp *Alpheus clypeatus* was pointed out by BOWERS (1971). He found that the algal tubes which the animals construct play a significant role in their pair formation and species spacing within the habitat. Presence of algae curtailed the shrimps' aggressive behaviour whilst enhancing the survival rate of their heterosexual pairs. BOWERS (*l. c.*) concluded that algal tubes provide the basis for a territorial social system which 1) allows the shrimps a higher population density, 2) increases the exploitable surface of their habitat.

4. 3 SUBSTRATE AND SHELTER

WALLNER (1935) published an hitherto unnoticed paper on interactions between lime-depositing algae and chironomid flies. He concluded that the presence of such algae enables the flies to initiate their colonization of fast-flowing streams. BROCK (1970), in his review on High Temperature Systems, included several instances of arthropods which live in algal mats in relatively hot (ca. 40° C) waters. A new method for mass- rearing the dipteran *Chironomus riparius* was described by CREDLAND (1973), a method based on the availability of more larval settling sites on filamentous algae maintained in plastic tanks. BARNARD (1972), who collected amphipods in New Zealand, noted that *Caulerpa* beds were especially rich in these animals, whereas *Hormosira* was generally a poor refuge for amphipods.

Tropical floating marine algae were observed by TEETER (1973) to accommodate some ostracods. These findings suggest an explanation for the transoceanic dispersal of ostracods within tropical latitudes (TEETER, *l. c.*). Another mode of ostracod dispersal may be while attached to sections of algae floating in water taken into bilge tanks of oil tankers and bulk-carrying ships during ballasting while sailing across the Panama Canal (TEETER 1973).

5. 1 NUTRIENT REGENERATION

CORNER and DAVIES (1971) reviewed the role of plankton in the nitrogen and phosphorus cycles taking place in the sea, and included diverse algal-arthropod grazing relationships. BROCK (1970) noted that colonization of algal mats by ephydrid flies promotes mat mineralization, usually a rather slow process.

The shells of diatoms ingested by some copepods are voided while encased within a membrane which protects the enclosed diatoms from dissolution during their descent to ocean floor (SCHRADER 1971). These pellets sink many times faster than a single shell, thus rapidly transporting silica from surface water to deeper layers. The process may deplete the upper waters of silica (and other nutrients), while delivering an abundance of this mineral to the ocean floor. Such excess extraction drives surface water toward undersaturation, until solution rates on the ocean floor provide the necessary balance for equilibrium of silica reservoirs in the ocean (SCHRADER, *l. c.*).

5.3 MUTUALISM AND SYMBIOSIS

WILLEY (1972) described the cycle of the euglenoid *Colacium* which inhabits damsel-fly hindguts in an interdunal pond in Indiana, U.S.A. During fall *Colacium* flagellates enter the insects' rectum by swimming directly through the anus. The alga later secretes a gelatinous material by which it is held to the rectal walls. Large *Colacium* colonies are then formed, which occur in the rectum of the damsel-fly naiads as green plugs, easily seen through the hosts' abdominal walls. In spring some *Colacium* cells leave the host organ with fecal pellets, but most are ejected with the rectal cuticle as it is cast off during molt. Damsel-fly naiads are not reinfected prior to emerging as adults.

Other observations on *Colacium* were published by ROSOWSKI and KUGRENS (1973). These authors were mainly concerned with the formation and morphology of attachment material, an important character in the taxonomy of *Colacium*. They suggested that structure and formation of attachment material produced by copepod-colonizing *Colacium* may be affected by concentrations of trace elements in the arthropods' exoskeleton.

Some additional observations on the *Nostoc-Cricotopus* mutualism were published by TODD (1971), while recording new algae from Colorado, U.S.A..

5.4 DISPERSAL

The mud dauber wasp, *Sceliphron caementarium*, and the cabbage butterfly, *Pieris protodice*, were shown by SIDES (1970, 1971) to transport viable algae (and protozoa). The algal cultures obtained were similar to those found by former investigators. It was concluded (SIDES, *l. c.*) that *Sceliphron* may be a relatively important carrier of algae and protozoa, but that the cabbage butterfly is only a minor vector. SOLON and STEWART (1972) reported that carnivorous insects such as dragonflies (Odonata), preying on other insects which live near water, may also transport viable algal cells, this dispersal being merely accidental or incidental.

ANDERSON, LEIDHAL and BRASHIER (1971) reported on the presence of viable algae in the anterior and posterior gut parts of the chironomid fly *Tendipes plumosa*. Presence of algae in the latter part suggests that they may also be dispersed by this midge.

Dissemination of viable algal propagules into the tissues of another plant by chironomid larvae was postulated by BERG (1950). That author found small larvae of *Cricotopus flavipes* excavating longitudinal mines in stems of the macrophyte *Potamogeton*. Viable algae, identified as *Nostoc, Anabaena* and others, were also found in the excavations. BERG (*l. c.*) thought it possible that the larvae had introduced the original algal propagules into the mines, where the algae were growing as rapidly as they were being eaten by the larvae.

6. 4 WATER BLOOMS AND TOXINS

O' BRIEN and DE NOYELLES (1972) reported on a pH-related mortality factor which affected cladocerans in nutrient-enriched ponds maintaining very high levels of primary production. Ryther's 1954 results were reinterpreted by O' BRIEN and DE NOYELLES (1972) as having been caused, in part, by a similar elevated pH mortality factor.

6. 5 THE BIOLOGICAL CONTROL OF MOSQUITOES BY ALGAE

A significant contribution in this area was made by AMONKAR (1969) in his Ph. D. thesis (later summarized by REEVES 1970). Amonkar isolated several algal cultures from southern California freshwater bodies in which natural control of mosquito larvae was apparently taking place. Cultures of *Cladophora glomerata* (denoted as culture AL-001), *Schizothrix friesii* (AL-003), *Chara fragilis* (AL-004), *Chlorella ellipsoidea* (AL-005) and *Chara elegans* (AL-010, AL-011, AL-012) exhibited marked larvicidal properties. The effects of these algae were assayed by their sterile, spent growth media whose usually alkaline reaction did not, by itself, affect the larvae. This indicates that the larvicidal activity is due to toxic substances which the algae release into the surrounding water (or culture medium).

The spent algal media (and purified concentrations prepared thereof) delayed mosquito egg hatching, reduced larval weights and, most significantly, proved to be highly larvicidal. AL-001 and AL-003 were the more toxic. Histopathological studies on mosquito larvae treated with the chromatographically-purified AL 001 toxic fraction revealed destructive effects on the epithelial lining of the alimentary canal. This damage disrupted normal food passage through the alimentary canal, causing leakage of gut contents into the haemocoel.

The toxin secreted by AL-001 is a heat-stable, non-dialyzable compound, whose ultraviolet and infra-red spectroscopic patterns suggest that it is an unsaturated organic substance with a nitrile group as well as terminal methylenes.

The active fraction from AL-003 appears to be a similar although different compound. The toxic secretions of AL-004, 010, 011 and 012 are identical, having sulfoxide and terminal methylene groups.

These natural toxins appear to be quite specific mosquito larvicides, as no adverse effects on other organisms - including water insects - could be detected in the original freshwater bodies. The findings of AMONKAR (1969) are therefore of wide practical importance, a point which he emphasized. He also reviewed most of the literature on algae which inhibit or kill mosquito larvae. Deleterious aspects of the use of algae to control mosquitoes were discussed by YEO (1972), who suggested that such algae - especially *Chara* and *Cladophora* may cause some aquatic nuisance problems.

The findings about a toxic substance secreted by *Cladophora glomerata* bring to mind results reported by ISHAC and BISHAI (1968) regarding the effect of this alga on *Biomphalaria boissyi*, the snail host of *Schistosoma mansoni*, the causal agent of bilharziasis. Growth of *C. glomerata* on the shells of the snails reduced the latters' fecundity as well as egg fertility and hatchability. ISHAC and BISHAI (*l. c.*) attributed these effects to presence of acrylic acid $CH^2{=}CH{-}COOH$) in *Cladophora*. The toxic compound isolated by AMONKAR (1969) from *C. glomerata* could thus have been a polymerization product of acrylic acid, whose carboxyl group was replaced by a cyanide to form a nitrile.

6. 8 INDIRECT EFFECTS OF HYDROLYZED SEAWEED

HAMSTEAD (1970) conducted two experiments with the hydrolyzed seaweed product Sea-Born$^{(R)}$, intended to control the two-spotted spider mite, *Tetranychus urticae*. In the first experiment a substancial decrease took place in the pest populations following applications of the seaweed hydrolysate and releases of a predaceous mite, as compared to predator releases combined with water sprays. In the second, more detailed experiment, no discernible decline in pest populations followed applications of Sea-Born$^{(R)}$ by itself.

7. 1 COMMUNITIES ON SEAWEED AND ON FRESHWATER ALGAE

Competition within an animal community living on algal belts in the Baltic Sea off the Swedish coast was studied by JANSSON (1969). She found that early in july the belts are colonized by juveniles of the isopods *Idotea baltica* and *I. chelipes* which feed on the algae and on sessile diatoms living thereon. Their feeding causes various competition patterns to occur among the isopods as well as among the rotifers and ciliates which live in the same community.

WIEGERT and MITCHELL (1973) studied the effect of algal mat stability on adult brine fly (*Paracoenia turbida*) parasitization by the water mite *Partnuniella thermalis*. The fly lives in and on mucilaginous mats formed by blue-green algae and bacteria in hot springs at Yellowstone National Park. *Paracoenia* has a short life cycle (14 days at 35° C), and its voracious larvae can rapidly destroy suitable mats. The mite, on the other hand, has a slower life cycle, consequently parasitizing its host-flies only in relatively stable mats. The mite-fly intersect (i. e., percent of flies parasitized and size of mite load on these flies) may therefore be used as a sensitive measure of mat stability.

7. 3 COMPETITION FOR SETTLING SITES

LIPKIN and SAFRIEL (1971), in their studies on the zonation of Mediterranean rocky shores at Mikhmoret, Israel, found that populations of the barnacle *Chthamalusstellatus* may be suppressed by algae in the mid-midlittoral intertidal zone. Individual barnacles may, however, survive under the algal cover.

7. 4 COMMUNITIES AFFECTED BY TECHNOLOGICAL CHANGES

Algal growth on flooded trees in the man-made Volta Lake (Ghana) supports a great abundance of the borrowing mayfly *Povilla adusta* (PETR 1971). The insects are heavily exploited by commercial fish. A man-made alga-insect-fish food chain, of considerable importance in the convertion of algae into animal protein, has thus evolved as a result of technological changes.

The pollution-associated disruption of invertebrate communities which live in kelp forest holdfasts in the North Sea was described by JONES (1973). He noted that many species (including numerous arthropods) have disappeared from these communities. Mechanical harvesting (raking) of Irish moss (*Chondrus crispus*) near Prince Edward Island damages many «moss»-associated lobsters, reducing their landed value by about 7% (SCARRATT 1973).

The reduction of herbivorous crustaceans by insecticide treatments of freshwater ponds was observed by HURLBERT, MULLA and WILLSON (1972) to be followed by phytoplankton increases to bloom dimensions.

7. 5 SOME GEOLOGICAL ASPECTS OF ALGA-ARTHROPOD ASSOCIATIONS.

Some copepods produce diatom-containing fecal pellets which are enclosed within a membrane (SCHRADER 1971). These pellets form deep-sea diatom sediments occuring down to 4000 m off the coast of Portugal. The diatoms would not have sunk by themselves, without being enclosed by the membrane, as they would have been completely dissolved before reaching such depths. This illustrates the role of copepod-produced fecal pellets in the sedimentation of pelagic diatoms.

8. 2 EFFECT OF INSECTICIDES ON ALGAE

Insecticide concentration in algae, the differential reaction of diverse algal species to insecticides, and effect of the resultant variable mortality (or inhibition) on aquatic ecosystems and food chains were discussed in some recent papers.

COX (1970) found that the level of DDT and some of its metabolites was tripled in phytoplankton samples collected off the Californian coast from 1955 to 1969. Several freshwater algae, such as *Anacystis nidulans*, *Scenedesmus obliquus* and *Euglena gracilis*, concentrated DDT 850, 630 and 100 fold, respectively, from their media (GREGORY, REED and PRIESTER 1969). The organophosphorus insecticide parathion was concentrated by these algae about 50-70 times. The ability of algae to retain and concentrate insecticides may have implications for control of pests which live in and feed on these plants. BURTON (1973) discussed such possibilities upon finding huge numbers of black fly (*Simulium*) larvae feeding exclusively on *Oedegonium* filaments in Ghana.

EGLOFF and PARTRIDGE (1972) showed that *Chlamydomonas reinhardtii* was not affected by concentrations of 100-1000 ppb of DDT. These authors speculated that such relatively-resistant species might displace less tolerant ones in polluted situations and thereby reduce or alter species composition in freshwater bodies exposed to insecticides.

This idea was experimentally explored by MOSSER, FISHER and WURSTER (1972). DDT or polychlorinated biphenyls were added to mixed cultures of the insecticide-susceptible diatom *Thalassiosira pseudonana* and the resistant green alga *Dunaliella tertiolecta*. In mixed control cultures the diatom grew faster and became dominant. But the dominance of *Thalassiosira* diminished on introducing the chemicals, even at concentrations that had no apparent effect when added to pure algal cultures. MOSSER et al. (*l. c.*) concluded that such stable pollulants «could profoundly affect the health, distribution and abundance of many animal populations higher in the food web». A more moderate opinion as to the effect of DDT on oceanic life was expressed by JUKES (1974).

The interactions of pesticides and algae were discussed within the context of pesticide-microorganism reviews by PFISTER (1972) and by WARE and ROAN (1970).

Several more technical papers on this subject were recently published in the Bulletin of Environmental Contamination and Toxicology but they are outside the scope of the present review.

9. 1 THE SCARCITY OF SYMBIOSIS

Doubts about the validity of the reported wide systematic range of invertebrate hosts for algae were expressed by TAYLOR (1973). He argued that most animals which participate in symbiotic associations with algae are characterized by a relatively low level of intercellular co-ordination. The introduction of alien cells into tissues of such invertebrates would do little to disrupt the animals' underlying organization. Further, these animals have low or non-existent immunological barriers. Cohabitation with algal cells thus causes little cellular difficulties for the host. TAYLOR (*l. c.*) also pointed out that the majority of symbiotic hosts are carnivores, hence less likely to be capable of digesting their associated algae. The establishment of symbiosis with herbivores probably depends upon algal resistance to digestion as well as increased host susceptibility.

These remarks go a long way towards explaining the scarcity of symbiosis between arthropods and algae. They cannot however apply to associations involving bacteria, yeasts and fungi, as these organisms often occur as symbiotes of insects, animals with highly developed cellular co-ordination. One thus feels that algae are rather different from other microorganisms in their relative suitability for symbiosis, as already suggested by DROOP (in main reference list).

TAYLOR (1973), as noted, pointed out that most invertebrates which host algae are carnivorous. It is therefore of interest that the only arthropods hitherto reported to have algal symbiotes are damsel flies, which are predaceous insects. It is of further interest that the symbiotic algae studied by WILLEY (1972) enter their host via its rectum, and those reported by SELVARAJ and JOB (in main reference list) live in the caudal lamellae of their host, near the main tracheal branches. The symbiotic algae are not very likely to be much affected by their hosts' digestive system in either case.

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